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**Dynamics of biomass and nutrient accumulation in rubber (*Hevea brasiliensis*) plantations established on two soil types: implications for nutrient management over the immature phase.**

Perron Thibaut<sup>1,2,+</sup>, Mareschal Louis<sup>3,4</sup>, Laclau Jean-Paul<sup>3,4</sup>, Deffontaines Lucie<sup>3,4</sup>, Deleporte Philippe<sup>3,4</sup>, Masson Aurélien<sup>5</sup>, Cauchy Thierry<sup>6</sup>, Gay Frédéric<sup>1,2</sup>

<sup>1</sup> CIRAD, UMR ABSys, F-34398 Montpellier, France

<sup>2</sup> ABSys, Univ Montpellier, CIHEAM-IAMM, CIRAD, INRAE, Institut Agro, Montpellier, France.

<sup>3</sup> CIRAD, UMR Eco&Sols, F-34398 Montpellier, France

<sup>4</sup> Eco&Sols, Univ. Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France.

<sup>5</sup> SoGB, Agricultural technique, auditing and Organisation Department (DTAO), SOCFIN, Ivory Coast

<sup>6</sup> Michelin, Agricultural Department, Ivory Coast

<sup>+</sup> Corresponding author: CIRAD, Avenue Agropolis, 34398 Montpellier Cedex 5, France.

E-mail address: [thibaut.perron@cirad.fr](mailto:thibaut.perron@cirad.fr) (T. Perron).

## I. Introduction

The rubber tree (*Hevea brasiliensis*) is the main source of natural rubber (NR). In order to meet the growing demand for NR, the area occupied by rubber plantations worldwide increased from 3.9 million ha in 1961 to 12.5 million ha in 2018 (FAO, 2020). The sustainability of latex production is a growing concern for the stakeholders of the NR value chain. Highly productive rubber plantations need to match the use of mineral fertilizers to the dynamics of the nutrient requirements of the trees, taking into account their availability in the soil (Vrignon-Brenas et al., 2019).

Although rubber trees are unproductive during the immature phase, from planting to about 6 years old, this period is critical for the future latex yields and the profitability of the plantation. The immature phase can be divided into two periods with regard to tree phenology and growth. The juvenile phase (from planting to 2 years old) is characterized by fast vertical growth, while the maturation period (from 2 years old up to latex collection at 6 years) is characterized by an acceleration of the radial growth of the stem (Compagnon, 1986; Vrignon-Brenas et al., 2019). The immature phase ends when 50% of the trees reach a trunk girth of 50 cm 1 m from the ground. Rubber trees are then tapped for latex production until they reach 25 to 40 years old. Management practices in immature plantations therefore seek to maximize the growth of the trees to start latex collection as early as possible.

NPK fertilizers are commonly used to increase the growth of immature rubber trees (Abraham et al., 2015; Alle et al., 2015; Samarappuli, 2000a). In a recent review of the literature, Vrignon-Brenas et al. (2019) showed huge ranges of fertilizer applications, from 27 to 697 kg ha<sup>-1</sup> yr<sup>-1</sup> for N, 29 to 326 kg ha<sup>-1</sup> yr<sup>-1</sup> for P and 14 to 232 kg ha<sup>-1</sup> yr<sup>-1</sup> for K, depending on local conditions. This review paper shows that most of these recommendations rely on local empirical experiences and that references on the dynamics of tree nutrient requirements over the immature phase are mostly old (Polinière and Van Brandt, 1964; Shorrocks, 1965a). Experience in fast-growing planted forests suggests that improving our knowledge of tree nutrient requirements throughout the early growth stages could help design more sustainable nutrient management plans for immature rubber plantations (Laclau et al., 2003; Laclau et al., 2010b). In tropical planted forests, nutrients accumulate differently throughout the rotation. N, P and K would seem to accumulate more during the early growth stage, while Ca and Mg accumulation is more linear throughout the lifespan of the plantation (Fernández-Moya et al., 2015). In the case of rubber trees, the consequences of fertilizer applications for the dynamics of nutrient accumulation in the trees has never been quantified over an entire rotation (35-40 years), as far as we are aware.

According to Vrignon-Brenas et al. (2019), logging residues ((i.e. trunks, branches, leaves, stumps and roots of the logged plantation) could be managed better to reduce the amounts

of fertilizers needed to address the problem of long-term fertility loss in rubber monocultures. Logging residues should be left on the soil surface after the clear-cutting of old stands. Even though no data are available for rubber plantations, the ways in which logging residue management affect tree growth have been abundantly studied in eucalyptus plantations. An isotopic study showed that logging residues provided 39% of tree N requirements over the first two years after planting in the Congo (Versini et al., 2014). In this sandy soil, a positive and strong relationship was established between the amount of logging residues left on site after harvesting and the aboveground biomass of eucalyptus trees at the end of the following rotation (Laclau et al., 2010a). Logging residue management practices particularly affect tree growth on low-fertility soils (Van Bich et al., 2019), and most rubber plantations are established on such soils.

The common practice in rubber cultivation is to burn or to export logging residues. Planters used to adopt these practices to limit the risk of root rot disease (Nandris et al., 1987), which can be a major constraint in rubber plantations (Ogbebor et al., 2013). However, the risk linked to root disease seems to be mainly observed over the first rotation of a rubber plantation, after conversion from forest. Burning or exporting residues is generally done nowadays for economic considerations. Residue burning remains the cheapest way of preparing land for large-scale plantations (Simorangkir, 2006). However, it was banned some decades ago in several countries for its adverse effects on air quality (Tomich et al., 1998) and nutrient losses through runoff and/or volatilization. The most common practice nowadays, in both industrial rubber plantations and smallholdings, is to export logging residues from plots to be used as timber, or for their heating value (Hytönen et al., 2019). Trunks, branches and stumps may be exported depending on the type of use, but leaves are generally left on site. Information on the nutrient stocks in tree components at the time of the clear-cut is therefore needed to assess the consequences of logging practices on soil nutrient depletion and on the amounts of nutrients available for the next rubber cycle.

Allometric equations are needed for an accurate estimation of the biomass and nutrient stocks in tree plantations (Picard et al., 2012). These equations link a predictive variable (biomass or nutrient stock of a given tree component) with an easily measurable dendrometric variable, such as tree height or trunk diameter. Many studies have already used allometric equations to estimate the biomass of rubber trees (Blagodatsky et al., 2016). However, to date, the dynamics of nutrient accumulation in tree components have never been studied over the complete cycle of a rubber plantation.

Our study set out to gain insights into the dynamics of nutrient accumulation over the complete plantation cycle of rubber trees growing in two regions with contrasting soil properties and fertilization practices. We focused on the following questions: (1) what are the consequences of contrasting management practices (for two clones planted on two soil

types) on nutrient accumulation in rubber trees? and (2) what is the impact of logging practices on the amounts of nutrients left on-site in logging residues at the clear-cutting of commercial rubber plantations?

## II. Materials and methods

### 2.1 Study sites

The study was carried out from October 2016 to January 2017 in two commercial rubber plantations located in Ivory Coast (Figure 1): the Toupah-Osrou plantation belonging to *Société Africaine des Plantations d'Hévéas* (SAPH), located in the South-East of the country (latitude 5°19'8.446"N, longitude 4°33'54.502"W, 54 m elevation) with 6,700 ha of rubber plantations, and *Société de Caoutchouc de Grand-Béréby* (SOGB), located in the South-West of the country (latitude 4°43'9.696"N, longitude 7°6'41.795"W, 34 m elevation) with 16,300 ha of rubber plantations. Both commercial plantations were established in the ecological zone of the rainforest, where a subequatorial climate suited to rubber tree cultivation prevailed. The rainfall regime in South Ivory Coast is divided into two rainy seasons, a major from May to July and a minor from October to November, and two dry seasons, from December to April and from August to September. Average annual rainfall from 2013 to 2018 was similar at SOGB (1674 mm) and SAPH (1718 mm). Mean monthly rainfall ranges from 40 to 451 mm at SAPH and from 48 to 581 mm at SOGB (Supplementary Figure 1).

Soil types and topographical conditions are different between the two sites, with mainly flat areas (<5% slope) and deep yellow ferrallitic Arenosol soils derived from tertiary sands at SAPH, while the SOGB site is characterized by hilly areas (10-25% slope) and gravel-rich red Ferralsol soils developed from schist and basalt. The soil texture in the upper layers is loamy sand at SAPH with 9% of clay on average, and sandy loam at SOGB with 22% of clay. The soils are acidic at both sites with an average  $\text{pH}_{\text{H}_2\text{O}}$  of about 5 in the upper horizons (Table 1). Overall, soil chemical fertility is better at SOGB than at SAPH, with a higher cation exchange capacity (CEC), total N and total C contents.

### 2.2 Plot selection

Changes in nutrient stocks throughout the rotation of a rubber plantation were studied using a chronosequence approach with 4 stand ages at each site. Four plots representative of commercial plantations were inventoried at each site and for each of the 4 stand ages. We selected plots at the end of the juvenile phase (2 years after planting) and at the end of the immature period (5 years after planting). We then selected 20-year-old stands, which is in the

middle of the latex production period in most commercial plantations in this region. Lastly, stands at the end of the cultural cycle (just before clear-cut) were sampled at 40 years old at SAPH and 38 years old at SOGB. All the stands in these chronosequences were planted with the GT1 clone at SAPH and the PB217 clone at SOGB. These clones are widespread in rubber plantations all over the world. Many studies observed that commercial clones had not significant effect on biomass accumulation in the tree. In a study conducted in Ghana including clones PB217 and GT1, Wauters et al. (2008) showed that variable “*clone type*” did not bring any significant improvement in the robustness of models for carbon stock estimation. In the same line, Chaudhuri et al. (1995) and Shorrocks et al. (1965) did not found any significant differences between allometric equations of different rubber clones of the same ages.

An inventory (on 500 to 858 trees) and destructive sampling of trees representing the different diameter classes in the stand were carried out in one plot (called the reference plot) out of the four plots per age studied at each site (cf. section 4). In the other three plots (called the additional plots), an inventory of the stand was carried out on 80 to 200 trees. The additional and reference plots of a given age were located within a 10-km radius. In total for SAPH and SOGB, 32 plots were inventoried measuring tree girth and quantifying the percentage of missing trees.

### 2.3 Crop management and stand characteristics

At SAPH, the tree density at planting ranged from 476 to 555 trees ha<sup>-1</sup> (Table 2). At SOGB, all the plots were planted at a density of 500 trees ha<sup>-1</sup>, except the 38-year-old plots with 555 trees ha<sup>-1</sup>. Two different planting designs were used at SOGB, either simple rows or double rows. Double-row spacing consists of inter-rows of 3 m and 13 m, alternately, while the inter-row remains the same for simple-row planting. Our inventories showed that the planting design in simple or double rows had little influence on tree growth. The survival rate in both the additional and reference plots ranged from 98 to 56% at SOGB and from 99 to 54% at the SAPH site. These survival rates were consistent with tree mortality rates due to wind damage and root diseases commonly observed throughout the entire rotation in commercial rubber tree plantations. The survival rate in the 5-year-old stand at SAPH (83% of living trees in the reference plot) was lower than expected at this age, due to a root infection caused by *Rigidoporus lignosus* that prevails in West Africa (Ogbebor et al., 2013).

At each site, all the plots sampled at each age received the same amount of mineral fertilizers. At SAPH, fertilizers were only applied in the first three years after planting for a total amount of 101, 31 and 106 kg ha<sup>-1</sup> for N, P and K, respectively. At SOGB, fertilizers were systematically applied every year up to 5 years after planting for a total amount of 300,

61 and 250 kg ha<sup>-1</sup> for N, P and K, respectively. Over the mature phase, from 6 years onwards, fertilization was applied depending on the latex production at SOGB, while no fertilizer was applied at SAPH.

Chemical weeding was carried out 4 to 6 times per year in immature stands and once a year in mature stands, 1 metre either side of the planting row. *Pueraria phaseoloides* was used as a cover crop in the inter-row during the immature phase at both sites to prevent soil erosion and to improve soil nitrogen status.

In mature stands at both sites, trees were tapped every 4 days for latex collection, 6 days a week (Sunday excluded), either in half spiral cut tapped downward or in quarter spiral cut tapped upward. Given the confidential nature of latex production in both rubber estates, nutrient exports in latex could not be considered in the present study.

## **2.4 Biomass and nutrient stocks in trees**

In the 2-, 5- and 20-year-old plots, 6 trees were selected for destructive measurements from 6 classes of basal area (i.e. 1 tree per class). In the oldest plots, 10 trees were selected from 10 classes of basal area. In total, 56 trees were destructively sampled to determine the biomass and nutrient concentrations in each component.

For each sampled tree, the height and circumference were measured (1 m from the ground for immature stands and 1.7 m for mature stands). The aboveground section was separated into three components, namely trunk, branches and leaves. Branches were considered as ramifications below 5 cm in diameter and the trunk consisted of the main stem and all ramifications above 5 cm in diameter. Due to the difficulty in observing the root system, 3 out of 6 trees for the aboveground components were sampled in the 2, 5 and 20-year-old stands, while all trees were sampled, both aboveground and belowground, in the 38-40 year-old plots (i.e. 10 trees). The stumps were uprooted down to a depth of 1 m and the lateral roots were sampled up to a diameter of 1 cm. The fresh weights of all the tree components were measured in the field. Subsamples of each component were collected and weighed for moisture content measurements. The samples were then oven dried (65°C) and crushed before chemical analyses. The P, K, Ca and Mg concentrations were determined using a spectrophotometer after digestion by hydrofluoric acid and double calcination. The N concentration was determined by the Kjeldahl method.

## **2.5 Allometric equations and data analysis**

We used log-transformed linear equations (Eq. 1) to investigate the relationship between the biomass of the tree components (leaves, trunk, branches and stump), or nutrient contents in each tree component, and a predictive variable:

$$\ln(y) = \ln(a) + b\ln(x) \quad (\text{Eq.1})$$

where  $y$  is the biomass or nutrient stock ( $\text{kg tree}^{-1}$ ),  $x$  the predictive variable,  $a$  the intercept coefficient, and  $b$  the scaling exponent.

To estimate the biomass and nutrient contents of each tree component, linear regressions were tested using diameter as the predictive variable. Diameter is the most commonly adopted predictive variable for biomass estimations in the case of the rubber tree (Wauters et al., 2008). Given the different clones and contrasting edaphic conditions between the study sites, the models were established at site level. The Akaike Information Criterion (AIC) and adjusted coefficient of determination (adj.  $R^2$ ) were used to select the best individual models. The model with the lowest AIC and highest adj.  $R^2$  was adopted. The selected models were applied to the stand inventory of both the reference and additional plots to assess the biomass and nutrient stock of each component.

The use of logarithmic equations might lead to an underestimation of the response variable  $y$  when converting  $\ln(y)$  to the untransformed scale  $y$ . To correct this bias, a correction factor (CF) was used for each allometric equation, as proposed by Baskerville (1972):

$$CF = \exp\left(\frac{RSE^2}{2}\right)$$

where RSE is the residual standard error of the model. The untransformed  $y$  was then obtained with the following equation:

$$y = e^a x^b + CF \quad (\text{Eq. 2})$$

For a given nutrient, the amount accumulated annually in the stand (expressed in  $\text{kg ha}^{-1} \text{yr}^{-1}$ ) between the ages  $n-1$  and  $n$  were then estimated with the following equation:

$$NAR = \frac{\text{nutrient stock}(age_n) - \text{nutrient stock}(age_{n-1})}{age_n - age_{n-1}} \quad (\text{Eq. 3})$$

where NAR is the mean nutrient accumulation rate between age  $n-1$  and age  $n$ .

The statistical analysis and allometric equations were carried out using RStudio software (RStudio Inc, Version 1.1463). The effect of stand age on nutrient concentrations as well as the effect of logging residue management on nutrient removal were investigated using analysis of variance (ANOVA). The normality of the model residuals and homoscedasticity of variances' residuals were checked prior the ANOVA. In the case of significant effect ( $p < 0.05$ ), Tukey HSD multiple comparisons of means (post-hoc test) was implemented, using the package *agricolae* (de Mendiburu, 2020).

### III. Results

#### 3.1 Allometric equations

In total, 48 allometric equations were fitted at the two study sites (Supplementary Table 1). They were used to predict the biomass and nutrient contents (N, P, K, Ca and Mg) in each tree component (leaves, branches, trunk and stump) from the stand inventories at each site. Figure 2 shows, as an example, the allometric equations developed to estimate the nitrogen contents in the tree components. The  $R^2$  value of the tree biomass models ranged from 0.83 to 0.98 at SAPH and from 0.56 to 0.98 at SOGB. On average, the models predicting tree nutrient stocks explained 86% and 75% of the variability at SAPH and SOGB, respectively.

#### 3.2 Dynamics of stand biomass accumulation

Tree biomass was 8.6, 51.2, 169.7 and 213.2 t ha<sup>-1</sup> at 2, 5, 20 and 40 years after planting at SAPH, respectively. The dynamics of tree biomass accumulation were similar at SOGB with 12.0, 47.9, 164.1 and 255.6 t ha<sup>-1</sup> at 2, 5, 20 and 38 years after planting, respectively (Figure 3). The highest current annual increment in biomass occurred between 2 and 5 years after planting, with stand biomass increasing by 493% (14.2 t ha<sup>-1</sup> yr<sup>-1</sup>) at SAPH and by 299% (12.0 t ha<sup>-1</sup> yr<sup>-1</sup>) at SOGB. Tree biomass at 5 years old accounted for about 20% of the standing biomass at the end of the plantation cycle. The share of trunk biomass in the total tree biomass kept increasing as the tree aged: from 33% at 2 years old to 64% at the clear-cut age at SAPH (from 31% to 74%, respectively, at SOGB). Conversely, the share of foliage within the total tree biomass sharply decreased from 14% in 2-year-old stands to 2% at the clear-cut age at both sites. To a lesser extent than for foliage, the share of stump and branches in the total biomass decreased as the tree aged.

#### 3.3 Nutrient concentrations

Regardless of tree age, the average N, P, K, Ca and Mg concentrations in tree components decreased following the ranking: Leaf > Branch > Stump > Trunk (Table 3). Changes in nutrient concentrations with tree age were consistent for the two chronosequences. While N, P and K concentrations in the aboveground tree components decreased from 2 to 20 years after planting (except in the leaves at SOGB), surprisingly, these concentrations tended to increase from 20 to 40 years after planting in most of the tree

components. Calcium concentrations increased with tree age in the ligneous tree components at both sites. The consequences of tree aging for Mg concentrations were less clear. The between-tree variability of nutrient concentrations in the stumps was high, which led to few significant differences between stand ages.

### 3.4 Dynamics of nutrient accumulation

The dynamics of N, P and K accumulation showed that the immature phase (the first 6 years after planting) was a period of intense nutrient uptake (Figure 4, Supplementary Figure 2). While the first 5 years covered only 12% of the plantation cycle, the amounts of N, P and K accumulated in the 5-year-old stands accounted for 25 to 36% of the total amounts at the clear-cut. N, P and K contents in the trees at 5 years old amounted to 291, 51 and 130 kg ha<sup>-1</sup>, respectively, at SAPH and 230, 29, and 177 kg ha<sup>-1</sup> at SOGB. The trunk was the main sink for N, P and K at 5 years old at both sites and the share of the trunk in the total accumulation of N, P and K in the trees increased sharply up to the end of the cycle. Large amounts of N, P and K were also accumulated in the branches and the stump at 5 years old, but these tree components contained a small proportion of the total accumulation in the trees at the clear-cut. While the accumulation of N, P and K in the trees remained large over the first half of the latex production phase (from 6 to 20 years after planting) at both sites (except for P at SOGB), the N, P and K contents in the trees increased much less over the second half of the cycle, in particular at SAPH. Before the clear-cut, the stocks of N, P and K in the tree components amounted to 970, 189, and 366 kg ha<sup>-1</sup>, respectively, at SAPH and 908, 118 and 628 kg ha<sup>-1</sup> at SOGB.

Unlike the sharp decrease in N, P and K accumulation as the trees aged, the dynamics of Ca accumulation continued steadily throughout the cycle (Figure 4). Only 15-17% of the total Ca content in the trees at the clear-cut was accumulated in 5-year-old stands (i.e. 163 kg ha<sup>-1</sup> at SAPH and 232 kg ha<sup>-1</sup> at SOGB). The accumulation pattern for Mg was intermediate between that of N, P and K, on the one hand, and that of Ca on the other hand (Supplementary Figure 2). Before the clear-cut, the amount of Ca accumulated in the trees was much higher at SOGB (1498 kg ha<sup>-1</sup>) than at SAPH (942 kg ha<sup>-1</sup>). The pattern was similar for Mg (374 kg ha<sup>-1</sup> at SOGB versus 256 kg ha<sup>-1</sup> at SAPH).

At both sites, the nutrient accumulation rates (NAR) in the trees peaked between 2 and 5 years after planting, regardless of the nutrient (Figure 5). Over this period, the highest rate of accumulation was for N at SAPH (80 kg ha<sup>-1</sup> yr<sup>-1</sup>), while Ca was the nutrient most accumulated in the trees at SOGB (58 kg ha<sup>-1</sup> yr<sup>-1</sup>), closely followed by N (53 kg ha<sup>-1</sup> yr<sup>-1</sup>).

After 5 years old, the NAR of all the nutrients continued to decrease at both sites up to the end of the plantation cycle.

### **3.5 Consequences of the fertilization regime for the immature phase**

From planting to 2 years old, the conventional NPK fertilization regimes in the rubber companies led to an input of nutrients to the soil that was much higher (from 30 to 167%) than the amounts accumulated in the trees (Table 2, Supplementary Table 3), except for Ca at SOGB (58 kg ha<sup>-1</sup> accumulated in trees vs 40 kg ha<sup>-1</sup> added through fertilization). The input of Mg to the soil through the addition of dolomite was 14 and 4 times higher than the amounts of Mg accumulated in the trees at SAPH and SOGB, respectively.

From 2 to 5 years after planting, the nutrient input to soil through fertilization at SAPH was 31, 9 and 34 kg ha<sup>-1</sup> of N, P and K, respectively. The accumulation of N, P and K in the trees over this period (240, 42 and 104 kg ha<sup>-1</sup>, respectively) was 8, 5 and 3 times higher than the amounts applied with fertilization (Table 2, Supplementary Table 3). Over the same period, the SOGB plots received 210, 43 and 173 kg ha<sup>-1</sup> of N, P, and K through fertilization, respectively. Unlike the plantations at SAPH, the inputs of N, P and K with fertilization exceeded the amounts accumulated in the trees during this period (161, 20 and 117 kg ha<sup>-1</sup> for N, P, and K, respectively).

## **IV. Discussion**

### **4.1 Biomass accumulation in rubber plantations**

The dynamics of biomass accumulation in our chronosequences were representative of highly productive rubber plantations worldwide. We found 14 references in the literature with estimates of biomass in rubber plantations, within the range of 2 to 40 years (Figure 6). Whilst the critical stage of biomass accumulation occurs over the early growth period, as shown in our study, there are very few references for immature stands (only 2 at 2 years old and 6 at 5 years old) compared with mature plantations. Some of the references (6 out of 14), mostly the older ones, did not use an accurate method to estimate stand biomass, but simply multiplied the biomass of the sampled trees by the stocking density. Inaccurate estimates (not using allometric relationships) might account for stand biomass values much higher than those at SAPH and SOGB reported in some studies. The variability in stand biomass in the literature might also be attributable to factors directly influencing tree growth related to inherent environmental parameters, such as climate (Munasinghe et al., 2014;

Wauters et al., 2008), elevation (Yang et al., 2017), but also related to management practices such as the stocking density and planting design (Wauters et al., 2008).

## **4.2 Dynamics of nutrient accumulation in tree components**

Each plantation has its own fertilization schedule built on empirical experience and it was not possible to sample stands with the same fertilization at the two sites. We compared two situations representative of commercial plantations in this study (with two clones in two soil types and two fertilization regimes). Our experimental does not make it possible to disentangle the effect of the clone from the effects of soil types and fertilization regimes in the dynamics of nutrient accumulations in the trees at the two sites. However, despite these differences, the consistent dynamics of nutrient accumulation in the trees at the two sites are an important finding of our study.

A large proportion of the N, P and K stocks in the trees at the clear-cut was accumulated over the early growth stage while Ca and Mg accumulation occurred linearly as the rubber tree aged. We showed that the rate of nutrient and biomass accumulation peaked very early after planting (between 2 and 5 years old). The dynamics of biomass accumulation in rubber tree components were characterized by a decrease in the share of leaf biomass and an increase in the share of trunk biomass within the total tree biomass as the plantation aged, thereby following the general trend for woody species (Miller, 1995). The fast N, P and K accumulation during early growth could be explained by the early development of nutrient-rich components, such as leaves and fine roots (not quantified in our study). The early growth stage of trees is indeed characterized by the maximum production of these two components acquiring the resources to achieve early dominance (Miller, 1995).

However, after the stand achieves its maximum leaf area, competition for light promotes the development of the trunk and branches, while the crown biomass is merely maintained or even decreases, as observed in our study. The trunk and branches, characterized by high Ca and Mg concentrations, became the main nutrient sinks. As the share of foliage in total tree biomass was less, N, P and K accumulation decreased and, conversely, Ca and Mg continued to accumulate, with the share of the trunk and branches becoming greater in the total tree biomass. In addition, mechanisms linked to nutrient retranslocations are largely involved in such nutrient accumulation dynamics. Rubber tree is a deciduous tree species that starts shedding its leaves from 4-5 years after planting. Leaf senescence leads to nutrient retranslocations from dying leaves to woody components, such as the trunk and branches. In rubber trees, approximately 50% of N, P and K from leaves is retranslocated to other tree components (Li et al., 2016). The strong biomass accumulation in the trunk and stump throughout the rotation with little internal remobilisation of Ca and Mg, as shown in

other woody species (Santos et al., 2017; Sette et al., 2013), probably leads to more regular accumulation throughout the cycle.

To our knowledge, the only study dealing with the dynamics of nutrient accumulation throughout the life span of a rubber plantation is Shorrocks (1965b). Our data on nutrient stocks were much lower than the latter study for all the sampling ages, e.g. for N stocks in 2-year-old stands, 51 kg N ha<sup>-1</sup> at SAPH vs 72 kg ha<sup>-1</sup> in Shorrocks (1965b), and at the clear-cut age, 970 kg N ha<sup>-1</sup> at SAPH vs 1779 kg ha<sup>-1</sup> in Shorrocks (1965b). These differences might be attributable to different methods of calculation, as detailed in section 4.1. The tendency regarding nutrient accumulation within the stand in Shorrocks (1965b) is in line with other studies carried out in fast-growing tree species for N and P (high accumulation over the early growth period) as well as Ca (linear accumulation). However, the accumulation of K was linear in Shorrocks (1965b), while most of the Mg accumulation occurred over the early growth period. The nutrient accumulation pattern in our study was consistent with other tropical tree species, such as teak in Central America (Fernández-Moya et al., 2015) and eucalyptus in Brazil (Sette et al., 2013). In other eucalypt plantations in the Congo, N, K and Ca followed the same dynamics as in our study, while a different pattern for Mg and P might reflect site-specific conditions with high soil P contents (Mareschal et al., 2011) and very low Mg bioavailability (Laclau et al., 2000).

#### **4.3 Influence of the fertilization regime and soil conditions on nutrient accumulation in trees**

The much larger amounts of fertilizer applied at SOGB than at SAPH did not necessarily increase nutrient accumulation in all the tree components. The dynamics of nutrient accumulation in trees showed two contrasting behaviours. The influence of nutrient bioavailability (in the soil and fertilizer inputs) on accumulation in the trees was weak for N, while the amounts of P, K, Ca and Mg accumulated in the trees at the end of the cycle reflected their bioavailability, either as exchangeable elements in the soil, or added as fertilizer. A meta-analysis for tropical tree species in planted forests highlighted a similar pattern, with phosphorus use efficiency to produce biomass that was much more variable than nitrogen use efficiency (Inagaki and Tange, 2014) (Figure 7). The latter study suggested that the accumulation of phosphorus in tree biomass depends more on soil conditions than on genetic factors, unlike nitrogen accumulation, as demonstrated by Fyllas et al. (2009). For Ca and Mg, a linear relationship between the accumulation of both nutrients in the trunk of eucalypt trees and soil Ca and Mg availability was shown for 45 stands in Brazil (Rocha et al., 2019). Research on plant physiology demonstrated that available P, K, Ca and Mg uptake rates - and consequently the concentration of these nutrients in the plant tissues -

continue to increase with an increase in the nutrient level in the soil solution (Gregory, 1996). This is consistent with the dynamics of accumulation in rubber trees in our study: the more P, K, Ca and Mg were available in the soil, the more these nutrients were taken up and accumulated in the trees.

We found that despite higher N and P fertilization at SOGB, the SAPH stands accumulated more of these two nutrients at 5, 20 and 40 years old. As the tree aged, the dependence of nutrient accumulation on soil nutrient availability and fertilization seemed to decrease, which may be due to alternative mechanisms. Firstly, it was demonstrated that biomass increments in nutrient-poor soils depends greatly on nutrient cycling from litter. In a study on poor Amazonian soils, Grau et al. (2017) demonstrated that N, P and K contents in the litter were positively correlated with the quadratic diameter. They hypothesized that nutrient uptake from litter could reduce the dependence of trees on soil nutrients in the context of nutrient-poor soils (Vitousek, 1984). In a 25-year-old rubber plantation in Ivory Coast, annual returns through litter fall amounted to 5.1 Mg ha<sup>-1</sup> yr<sup>-1</sup> (N'Dri et al., 2018). Litter decomposition results in substantial nutrient fluxes, which are decisive for the productivity of rubber plantations (Gréggio et al., 2008; Jessy et al., 2009). Further studies are needed for rubber trees to ascertain to what extent the nutrients released from leaf decomposition participate in nutrient accumulation within tree biomass.

Secondly, nutrient retranslocation increases with tree aging (Millard and Grelet, 2010) and this mechanism supplies a considerable amount of nutrients for tree growth. In an old Corsican pine plantation, it was shown that 50% of N and 68% of K was supplied through retranslocation for new growth, as opposed to 16% and 24%, respectively, in young plantations (Miller, 1995). For nutrient cycling from litter, retranslocation has been suggested as a plausible mechanism for reducing the dependency of tree growth on direct nutrient uptake in a context of poor-nutrient soils (Grau et al., 2017; Sardans and Peñuelas, 2015). There are very few studies dealing with nutrient retranslocations in rubber trees in the literature and further research is needed to quantify the amounts of nutrients retranslocated in different contexts of soil nutrient availability. Lastly, the higher N and P accumulation in the SAPH stands beyond 5 years old compared with SOGB suggested that other sources of nutrients (in addition to fertilizers) met the nutrient requirements of the trees. Among other things, atmospheric N fixation by the cover crop (Clermont-Dauphin et al., 2005), wet and dry deposits (Shorrocks, 1965a), mineralisation of soil organic matter and decomposition of tree residues from the previous crop cycle (Yew, 2001) play important roles in tree nutrition. This emphasises the need to take into account the overall nutrient inputs and outputs in the soil, as well as the stocks of bioavailable nutrients and the dynamics of tree requirements, to design appropriate fertilization programmes (Ranger and Turpault, 1999). However, the biogeochemical cycles of nutrients are still poorly documented in rubber plantations, which is

a considerable hindrance for establishing relevant fertilization regimes throughout the life span of rubber trees (Vrignon-Brenas et al., 2019).

#### **4.4 Consequences for managing logging residues**

Exports of residues for timber use only concerned the trunk (scenario 1, Table 4), while both the trunk and the branches were harvested for heating use (scenario 2, Table 4). These two residue management are the most implemented in rubber plantations and led to considerable exports of nutrients: between 42 and 88% of the nutrient stocks in the trees were removed depending on the nutrient and the site (Table 4).

In agreement with meta-analyses in forest areas (Achat et al., 2015; Wan et al., 2018), our study suggested that leaving logging residues on site could enhance the growth of replanted trees over the next rotation, especially in low-fertility soils. In rubber plantations, logging residues are commonly harvested for economic benefits, either as timber (Shigematsu et al., 2013), or as firewood for their heating value (Hytönen et al., 2019). Exporting off-site the large nutrient stocks contained in logging residues might negatively affect soil fertility (Watson, 1964; Webster, 1989) and the sustainability of future rotations established on nutrient-poor soils, as shown in tropical forest plantations (Laclau et al., 2010a; Legout et al., 2020; Versini et al., 2014). In addition to nutrient exports, the removal of logging residues can reduce C stocks in the topsoil, which can affect soil biological activity and the long-term sustainability of tropical plantations. Recent studies in Brazil and the Congo showed that the removal of harvest residues over 2-3 rotations in tropical eucalypt plantations can reduce C stocks in the topsoil (0-5 cm layer) by 40-50% (Epron et al., 2015; Rocha et al., 2018). Removing logging residues decreased the enzyme activities and catabolic potential of the soil microbial community in a Brazilian Ferralsol, suggesting that exporting all the logging residues could be harmful to soil health in tropical plantations (Maillard et al., 2019).

The amounts of nutrients exported off-site if the whole tree was harvested (scenario 4, Table 4) were greater than the total amounts applied as fertilisation over the cycle in both companies. In this scenario at SAPH, where fertilizer applications stopped 3 years after planting, the stocks of N, P, K, Ca and Mg exported accounted for 120-960% of the nutrient input through fertilization. At SOGB, the amount of nutrient removed after exporting residues in scenario 4 accounted for 193-1126% of N, P, K, Ca and Mg fertilization applied from planting to 5 years old. At the clear-cut stage, the N, P and K exported via logging residues accounted for 44-99% of N, P and K fertilization applied over the entire plantation cycle.

The ability of rubber trees to take up the nutrients released during residue decomposition is still poorly understood. While the decomposition of logging residues is rapid in rubber

plantations, the nutrient accumulation rates show that tree requirements are not linear over the immature phase, with higher demand between 2 and 5 years after planting. Few studies have dealt with the dynamics of nutrient releases throughout the decomposition of logging residues in rubber plantations. Yew (2001) provided some primary information regarding the decay time for different tree components, but that study did not provide precise decomposition kinetics making it possible to quantify nutrient releases. In eucalypt plantations, while some studies in Brazil showed that immobilisation within logging residues could postpone the release of nutrients relative to tree nutrient needs (Ferreira et al., 2016; Rocha et al., 2016), an isotopic study in the Congo showed that approximately 40% of the N content in 2-year-old eucalyptus trees was derived from the labelled logging residues (Versini et al., 2014). Further studies quantifying the release of nutrients in different types of logging residues, as well as the dynamics of soil exploration by fine roots after replanting, are needed to help improve nutrient management practices after replanting in immature rubber plantations.

## **V. Conclusion**

Our study shows consistent dynamics of nutrient accumulation throughout the growth of rubber trees in plantations established at two sites with two clones and contrasting fertilization practices. Nutrient accumulation rate peaked between 2 and 5 years after planting. While 25 to 36% of the stocks of N, P and K in the trees at the clear-cut stage were already accumulated at 5 years old, the accumulation of Ca was steady over the entire cycle of 40 years and the behaviour was intermediate for Mg. After the immature phase, recycling processes in addition to an increasing proportion of the trunk (with low concentrations of N, P, K) in total biomass, could account for the accumulation dynamics observed. Our study shows that logging practices can greatly influence the amounts of nutrients left on-site at the clear-cut stage, which could greatly influence soil fertility for the next rotation. The amount of nutrients removed in the case of whole-tree harvesting could account for 120-960% and 44-99% of the fertilization input over the entire rotation at SAPH and SOGB respectively. However, knowledge gaps need to be investigated to design more sustainable nutrient management strategies in immature rubber plantations. A precise assessment of nutrient input-output budgets over the immature phase is needed to improve the current fertilizer programmes. Information on the kinetics of nutrient release from logging residues is also needed to assess to what extent logging residues could replace fertilizers in the first years after planting.

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534

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538

539 **Conflict of interests**

540 The authors declare that they have no conflict of interests.

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## 542 References

- 543 Abraham, J., Joseph, K., Joseph, P., 2015. Effect of integrated nutrient management on soil  
544 quality and growth of hevea brasiliensis during the immature phase. *Rubber Science*  
545 28, 159–167.
- 546 Achat, D.L., Deleuze, C., Landmann, G., Pousse, N., Ranger, J., Augusto, L., 2015.  
547 Quantifying consequences of removing harvesting residues on forest soils and tree  
548 growth – A meta-analysis. *Forest Ecology and Management* 348, 124–141.  
549 <https://doi.org/10.1016/j.foreco.2015.03.042>
- 550 Alle, J.Y., Dick, E.A., Soumahin, E.F., Gabla, R.O., Keli, J.Z., Obouayeba, S., 2015. Effect of  
551 mineral fertilization on agrophysiological parameters and economic viability of clone  
552 PB 235 of *Hevea brasiliensis* in the region of GO in south western Cote d'Ivoire.  
553 [WWW Document]. *Journal of Animal and Plant Sciences (JAPS)*. URL  
554 <http://www.m.elewa.org/JAPS/2015/24.2/3.pdf>
- 555 Baskerville, G.L., 1972. Use of Logarithmic Regression in the Estimation of Plant Biomass.  
556 *Canadian Journal of Forestry* 2, 5.
- 557 Blagodatsky, S., Xu, J., Cadisch, G., 2016. Carbon balance of rubber (*Hevea brasiliensis*)  
558 plantations: A review of uncertainties at plot, landscape and production level.  
559 *Agriculture, Ecosystems & Environment* 221, 8–19.  
560 <https://doi.org/10.1016/j.agee.2016.01.025>
- 561 Chaudhuri, D., Vinod, K., Potty, S.N., Sethuraj, M.R., Pothan, J., Reddy, Y.A.N., 1995.  
562 Estimation of biomass in hevea clones by regression method: relation between girth  
563 and biomass. *Indian Journal of Natural Rubber Research* 8, 113–116.
- 564 Clermont-Dauphin, C., Cabidoche, Y.-M., Meynard, J.-M., 2005. Diagnosis on the  
565 sustainability of an upland cropping system of southern Haiti. *Agriculture, Ecosystems*  
566 *& Environment* 105, 221–234. <https://doi.org/10.1016/j.agee.2004.03.008>
- 567 Compagnon, P., 1986. L'hévéa et son milieu, in: *Le Caoutchouc Naturel : Biologie, Culture,*  
568 *Production.* G.P. Maisonneuve et Larose, p. 595.
- 569 de Mendiburu, P., 2020. Package “agricolae.”
- 570 Epron, D., Mouanda, C., Mareschal, L., Koutika, L.-S., 2015. Impacts of organic residue  
571 management on the soil C dynamics in a tropical eucalypt plantation on a nutrient-  
572 poor sandy soil after three rotations. *Soil Biology and Biochemistry* 85, 183–189.  
573 <https://doi.org/10.1016/j.soilbio.2015.03.010>
- 574 FAO, 2020. FAOSTAT [WWW Document]. URL <http://www.fao.org/faostat/en/#home>  
575 (accessed 4.24.20).
- 576 Fernández-Moya, J., Murillo, R., Portuguez, E., Fallas, J., Ríos, V., Kottman, F., Verjans, J.,  
577 Mata, R., Alvarado, A., 2015. Nutrient accumulation and export in teak (*Tectona*  
578 *grandis* L.f.) plantations of Central America. *iForest - Biogeosciences and Forestry* 8,  
579 33–44. <https://doi.org/10.3832/ifor1089-007>
- 580 Ferreira, G.W.D., Soares, E.M.B., Oliveira, F.C.C., Silva, I.R., Dungait, J.A.J., Souza, I.F.,  
581 Vergütz, L., 2016. Nutrient release from decomposing *Eucalyptus* harvest residues  
582 following simulated management practices in multiple sites in Brazil. *Forest Ecology*  
583 *and Management* 370, 1–11. <https://doi.org/10.1016/j.foreco.2016.03.047>
- 584 Fyllas, N.M., Schwarz, M., Horna, V., Mercado, L.M., Santos, A., Arroyo, L., Jimenez, E.M.,  
585 Luizao, F.J., Neill, D.A., Silva, N., Prieto, A., Rudas, A., Silviera, M., Vieira, I.C.G.,  
586 Lopez-Gonzalez, G., Malhi, Y., Phillips, O.L., Lloyd, J., 2009. Basin-wide variations in  
587 foliar properties of Amazonian forest: phylogeny, soils and climate 32.
- 588 Grau, O., Peñuelas, J., Ferry, B., Freycon, V., Blanc, L., Desprez, M., Baraloto, C., Chave,  
589 J., Descroix, L., Dourdain, A., Guitet, S., Janssens, I.A., Sardans, J., Hérault, B.,  
590 2017. Nutrient-cycling mechanisms other than the direct absorption from soil may  
591 control forest structure and dynamics in poor Amazonian soils. *Scientific Reports* 7.  
592 <https://doi.org/10.1038/srep45017>
- 593 Gréggio, T.C., Assis, L.C., Nahas, E., 2008. Decomposition of the rubber tree *Hevea*  
594 *brasiliensis* litter at two depths. *Chilean Journal of Agricultural Research* 68, 128–135.

- Gregory, P.J., 1996. Soil Nutrient Bioavailability: A Mechanistic Approach (2nd edition). The Journal of Agricultural Science 126, 250–251. <https://doi.org/10.1017/S0021859600073238>
- Hytönen, J., Nurmi, J., Kaakkurivaara, N., Kaakkurivaara, T., 2019. Rubber Tree (*Hevea brasiliensis*) Biomass, Nutrient Content, and Heating Values in Southern Thailand. Forests 10, 638. <https://doi.org/10.3390/f10080638>
- Inagaki, M., Tange, T., 2014. Nutrient accumulation in aboveground biomass of planted tropical trees: a meta-analysis. Soil Science and Plant Nutrition 60, 598–608. <https://doi.org/10.1080/00380768.2014.929025>
- Jessy, M.D., Nair, A.N.S., Bai, M.M., Rajendran, P., Punnoose, K.I., 2009. Self-sustainability of phosphorus cycle in rubber (*Hevea brasiliensis*) plantations: annual recycling through litter and removal through latex. Journal of Plantation Crops.
- Laclau, J.-P., Bouillet, J.-P., Ranger, J., 2000. Dynamics of biomass and nutrient accumulation in a clonal plantation of *Eucalyptus* in Congo. Forest Ecology and Management 128, 181–196. [https://doi.org/10.1016/S0378-1127\(99\)00146-2](https://doi.org/10.1016/S0378-1127(99)00146-2)
- Laclau, J.-P., Levillain, J., Deleporte, P., Nzila, J. de D., Bouillet, J.-P., Saint André, L., Versini, A., Mareschal, L., Nouvellon, Y., Thongo M'Bou, A., Ranger, J., 2010a. Organic residue mass at planting is an excellent predictor of tree growth in *Eucalyptus* plantations established on a sandy tropical soil. Forest Ecology and Management 260, 2148–2159. <https://doi.org/10.1016/j.foreco.2010.09.007>
- Laclau, J.-P., Ranger, J., de Moraes Gonçalves, J.L., Maquère, V., Krusche, A.V., M'Bou, A.T., Nouvellon, Y., Saint-André, L., Bouillet, J.-P., de Cassia Piccolo, M., Deleporte, P., 2010b. Biogeochemical cycles of nutrients in tropical *Eucalyptus* plantations. Forest Ecology and Management 259, 1771–1785. <https://doi.org/10.1016/j.foreco.2009.06.010>
- Laclau, J.-P., Ranger, J., Nzila, J. de D., Bouillet, J.-P., Deleporte, P., 2003. Nutrient cycling in a clonal stand of *Eucalyptus* and an adjacent savanna ecosystem in Congo. Forest Ecology and Management 180, 527–544. [https://doi.org/10.1016/S0378-1127\(02\)00645-X](https://doi.org/10.1016/S0378-1127(02)00645-X)
- Legout, A., Hansson, K., van der Heijden, G., Laclau, J.-P., Mareschal, L., Nys, C., Nicolas, M., Saint-André, L., Ranger, J., 2020. Chemical fertility of forest ecosystems. Part 2: Towards redefining the concept by untangling the role of the different components of biogeochemical cycling. Forest Ecology and Management 461, 117844. <https://doi.org/10.1016/j.foreco.2019.117844>
- Li, Y., Lan, G., Xia, Y., 2016. Rubber Trees Demonstrate a Clear Retranslocation Under Seasonal Drought and Cold Stresses. Frontiers in Plant Science 07. <https://doi.org/10.3389/fpls.2016.01907>
- Maillard, F., Leduc, V., Bach, C., de Moraes Gonçalves, J.L., Androte, F.D., Saint-André, L., Laclau, J.-P., Buée, M., Robin, A., 2019. Microbial Enzymatic Activities and Community-Level Physiological Profiles (CLPP) in Subsoil Layers Are Altered by Harvest Residue Management Practices in a Tropical *Eucalyptus grandis* Plantation. Microbial Ecology 78, 528–533. <https://doi.org/10.1007/s00248-018-1298-6>
- Mareschal, L., Nzila, J.D.D., Turpault, M.P., Thongo M'Bou, A., Mazoumbou, J.C., Bouillet, J.P., Ranger, J., Laclau, J.P., 2011. Mineralogical and physico-chemical properties of Ferralic Arenosols derived from unconsolidated Plio-Pleistocene deposits in the coastal plains of Congo. Geoderma 162, 159–170. <https://doi.org/10.1016/j.geoderma.2011.01.017>
- Millard, P., Grelet, G. -a., 2010. Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. Tree Physiology 30, 1083–1095. <https://doi.org/10.1093/treephys/tpq042>
- Miller, H.G., 1995. The influence of stand development on nutrient demand, growth and allocation. Plant and Soil 168–169, 225–232.
- Munasinghe, E.S., Rodrigo, V.H.L., Gunawardena, U.A.D.P., 2014. Modus operandi in assessing biomass and carbon in rubber plantations under varying climatic

- conditions. *Experimental Agriculture* 50, 40–58.  
<https://doi.org/10.1017/S0014479713000410>
- Nandris, D., Nicole, M., Geiger, J.P., 1987. Root rot diseases. *Plant Disease* 71, 298–306.
- N'Dri, J.K., Guéi, A.M., Edoukou, E.F., Yéo, J.G., N'Guessan, K.K., Lagerlöf, J., 2018. Can litter production and litter decomposition improve soil properties in the rubber plantations of different ages in Côte d'Ivoire? *Nutrient Cycling in Agroecosystems* 111, 203–215. <https://doi.org/10.1007/s10705-018-9923-9>
- Ogbebor, N.O., Adekunle, A.T., Eghafona, O.N., Ogboghodo, A.I., 2013. Incidence of *Rigidoporus lignosus* (Klotzsch) imaz of para rubber in Nigeria. *Researcher* 5, 181–184.
- Picard, N., Saint-André, L., Henry, M., 2012. Manual for building tree volume and biomass allometric equations from field measurement to prediction. Food and Agriculture Organization of the United Nations (FAO), Rome.
- Polinière, J.P., Van Brandt, H., 1964. Bilan des mouvements en éléments minéraux sous cultures d'hévéas au Viet-nam. *Revue Générale du Caoutchouc* 41, 1665–1672.
- Ranger, J., Turpault, M.-P., 1999. Input–output nutrient budgets as a diagnostic tool for sustainable forest management. *Forest Ecology and Management* 122, 139–154.
- Rocha, J.H.T., Gonçalves, J.L. de M., Brandani, C.B., Ferraz, A. de V., Franci, A.F., Marques, E.R.G., Arthur Junior, J.C., Hubner, A., 2018. Forest residue removal decreases soil quality and affects wood productivity even with high rates of fertilizer application. *Forest Ecology and Management* 430, 188–195. <https://doi.org/10.1016/j.foreco.2018.08.010>
- Rocha, J.H.T., Marques, E.R.G., Gonçalves, J.L. d. M., Hübner, A., Brandani, C.B., Ferraz, A. d. V., Moreira, R.M., 2016. Decomposition rates of forest residues and soil fertility after clear-cutting of *Eucalyptus grandis* stands in response to site management and fertilizer application. *Soil Use and Management* 32, 289–302. <https://doi.org/10.1111/sum.12283>
- Samarappuli, L., 2000a. Economics and efficiency of fertilizer utilization in immature rubber. *Bulletin of the Rubber Research Institute of Sri Lanka* 42, 1–10.
- Samarappuli, L., 2000b. Rubber growing soils and their characteristics. *Bulletin of the Rubber Research Institute of Sri Lanka* 41, 10–21.
- Santos, F.M., Chaer, G.M., Diniz, A.R., Balieiro, F. de C., 2017. Nutrient cycling over five years of mixed-species plantations of *Eucalyptus* and *Acacia* on a sandy tropical soil. *Forest Ecology and Management* 384, 110–121. <https://doi.org/10.1016/j.foreco.2016.10.041>
- Sardans, J., Peñuelas, J., 2015. Trees increase their P:N ratio with size. *Global Ecology and Biogeography* 24, 147–156. <https://doi.org/10.1111/geb.12231>
- Sette, C.R., Laclau, J.-P., Tomazello Filho, M., Moreira, R.M., Bouillet, J.-P., Ranger, J., Almeida, J.C.R., 2013. Source-driven remobilizations of nutrients within stem wood in *Eucalyptus grandis* plantations. *Trees* 27, 827–839. <https://doi.org/10.1007/s00468-012-0837-x>
- Shigematsu, A., Mizoue, N., Kakada, K., Muthavy, P., Kajisa, T., Yoshida, S., 2013. Financial potential of rubber plantations considering rubberwood production: Wood and crop production nexus. *Biomass and Bioenergy* 49, 131–142. <https://doi.org/10.1016/j.biombioe.2012.12.011>
- Shorrocks, V.M., 1965a. Mineral nutrition, growth and nutrient cycle of *Hevea brasiliensis*. Nutrient cycle and fertiliser requirements. *Journal of the Rubber Research Institute of Malaysia* 19, 48–61.
- Shorrocks, V.M., 1965b. Mineral nutrition, growth and nutrient cycle of *Hevea brasiliensis*. Growth and nutrient content. *Journal of the Rubber Research Institute of Malaysia* 19, 32–47.
- Shorrocks, V.M., Templeton, J.K., Iyer, G.C., 1965. Mineral nutrition, growth and nutrient cycle of *Hevea brasiliensis* III. The relationship between girth and shoot dry weight. *Journal of Rubber Research Institute of Malaysia* 19, 85–92.

- Simorangkir, D., 2006. Fire use: Is it really the cheaper land preparation method for large-scale plantations? *Mitigation and Adaptation Strategies for Global Change* 12, 147–164. <https://doi.org/10.1007/s11027-006-9049-2>
- Tomich, T., Fagi, A., de Foresta, H., Michon, G., Murdiyarso, D., Stolle, F., Van Noordwijk, M., 1998. Indonesia's fires: smoke as a problem, smoke as a symptom. *Agroforestry Today* 10, 4–7.
- Van Bich, N., Mendham, D., Evans, K.J., Dong, T.L., Hai, V.D., Van Thanh, H., Mohammed, C.L., 2019. Effect of residue management and fertiliser application on the productivity of a *Eucalyptus* hybrid and *Acacia mangium* planted on sloping terrain in northern Vietnam. *Southern Forests: a Journal of Forest Science* 81, 201–212. <https://doi.org/10.2989/20702620.2018.1555940>
- Versini, A., Zeller, B., Derrien, D., Mazoumbou, J.-C., Mareschal, L., Saint-André, L., Ranger, J., Laclau, J.-P., 2014. The role of harvest residues to sustain tree growth and soil nitrogen stocks in a tropical *Eucalyptus* plantation. *Plant and Soil* 376, 245–260. <https://doi.org/10.1007/s11104-013-1963-y>
- Vitousek, P.M., 1984. Litterfall, Nutrient Cycling, and Nutrient Limitation in Tropical Forests. *Ecology* 65, 285–298. <https://doi.org/10.2307/1939481>
- Vrignon-Brenas, S., Gay, F., Ricard, S., Snoeck, D., Perron, T., Mareschal, L., Laclau, J.-P., Gohet, É., Malagoli, P., 2019. Nutrient management of immature rubber plantations. A review. *Agronomy for Sustainable Development* 39. <https://doi.org/10.1007/s13593-019-0554-6>
- Wan, X., Xiao, L., Vadeboncoeur, M.A., Johnson, C.E., Huang, Z., 2018. Response of mineral soil carbon storage to harvest residue retention depends on soil texture: A meta-analysis. *Forest Ecology and Management* 408, 9–15. <https://doi.org/10.1016/j.foreco.2017.10.028>
- Watson, G.A., 1964. Maintenance of soil fertility in the permanent cultivation of *Hevea brasiliensis* in Malaya. *Outlook on Agriculture* 4, 103–109.
- Wauters, J.B., Coudert, S., Grallien, E., Jonard, M., Ponette, Q., 2008. Carbon stock in rubber tree plantations in Western Ghana and Mato Grosso (Brazil). *Forest Ecology and Management* 255, 2347–2361. <https://doi.org/10.1016/j.foreco.2007.12.038>
- Webster, C.C., 1989. Preparation of land for planting and replanting, in: *Rubber*. CC Webster & WJ Baulkwill, pp. 165–194.
- Yang, X., Blagodatsky, S., Liu, F., Beckschäfer, P., Xu, J., Cadisch, G., 2017. Rubber tree allometry, biomass partitioning and carbon stocks in mountainous landscapes of subtropical China. *Forest Ecology and Management* 404, 84–99. <https://doi.org/10.1016/j.foreco.2017.08.013>
- Yew, F.K., 2001. Impact of Zero Burning on Biomass and Nutrient Turnover in Rubber Replanting. *Malaysian Journal of Soil Science* 5, 19–26.

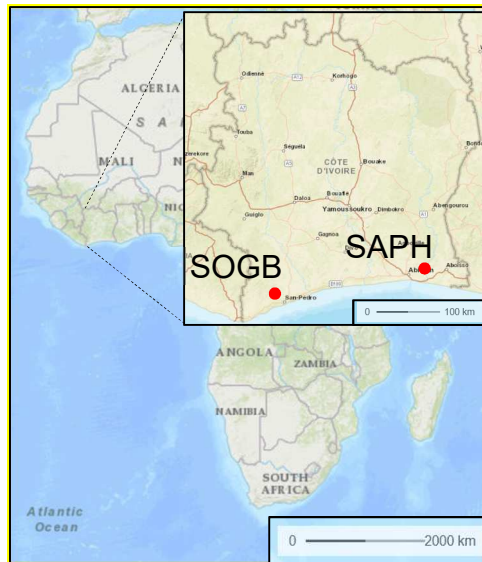


Figure 1: Map of Ivory Coast showing the geographical location of the study sites.

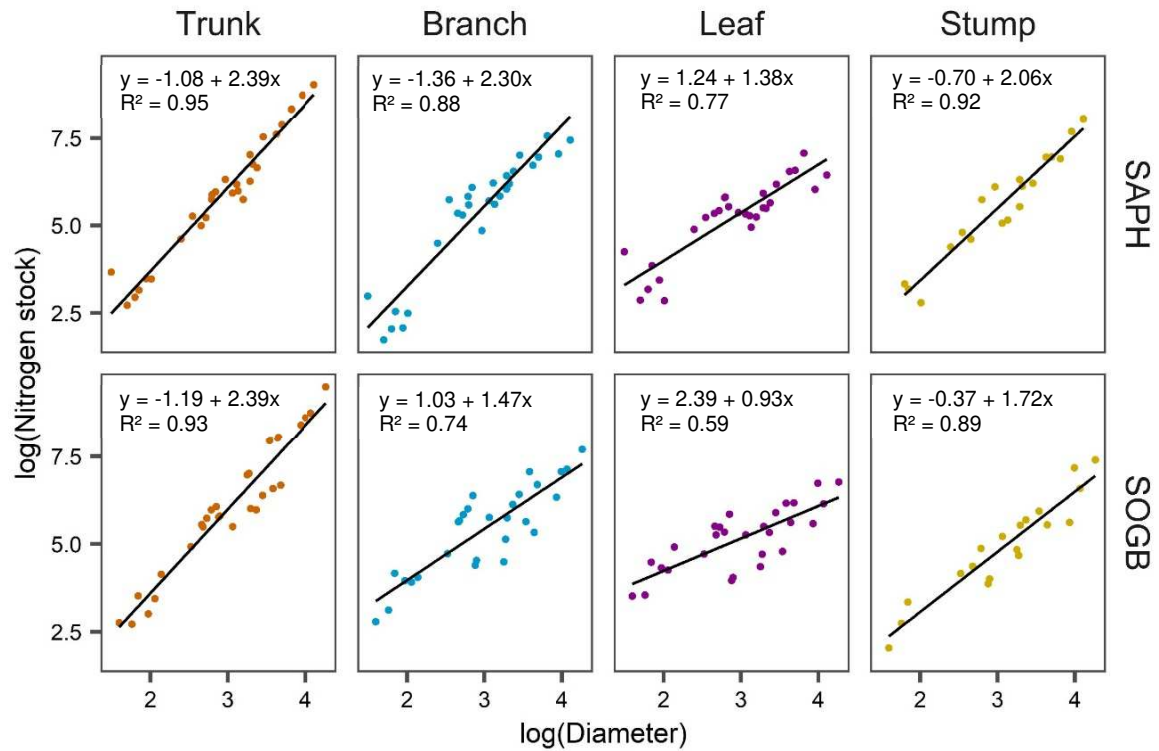


Figure 2: Log-transformed relationships between tree nitrogen stock ( $\text{g tree}^{-1}$ ) and tree diameter (cm) within tree components at SAPH and SOGB. At each site,  $n=28$  for branches, leaves and trunk;  $n=19$  for stumps.

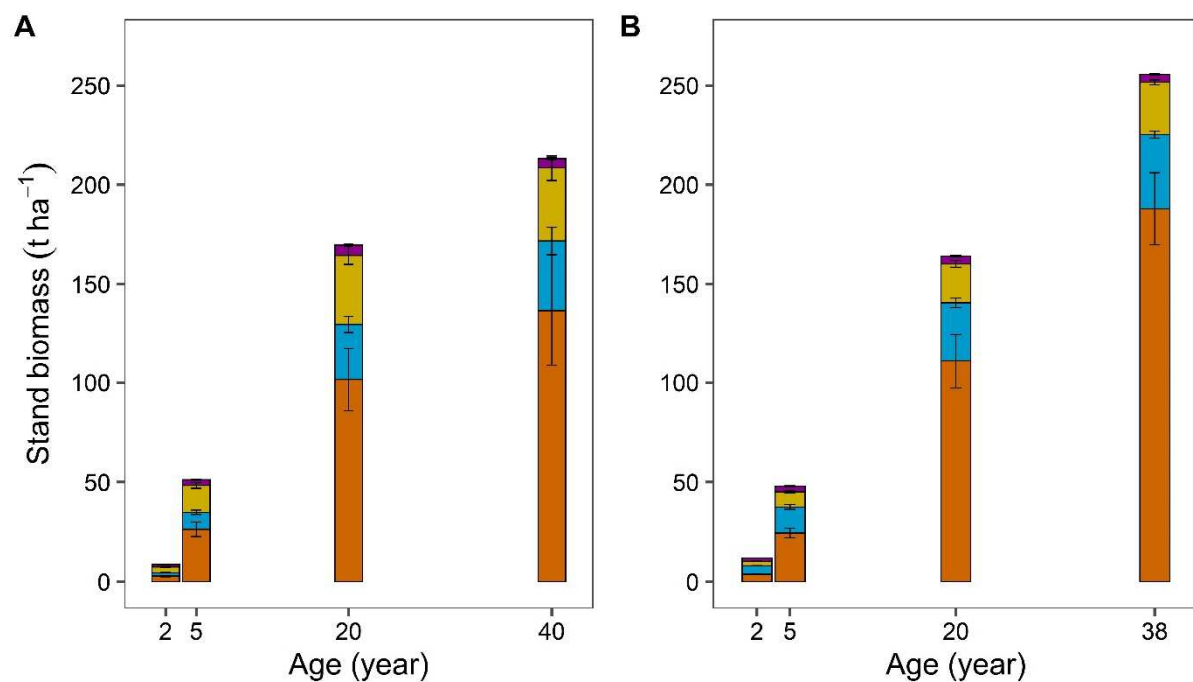


Figure 3: Dynamics of biomass accumulation (t ha<sup>-1</sup>) within tree components throughout the chronosequence at SAPH (A) and SOGB (B) obtained from the allometric equations. Standard deviations between the inventoried stands are indicated for each tree component (n=4).

Caption:



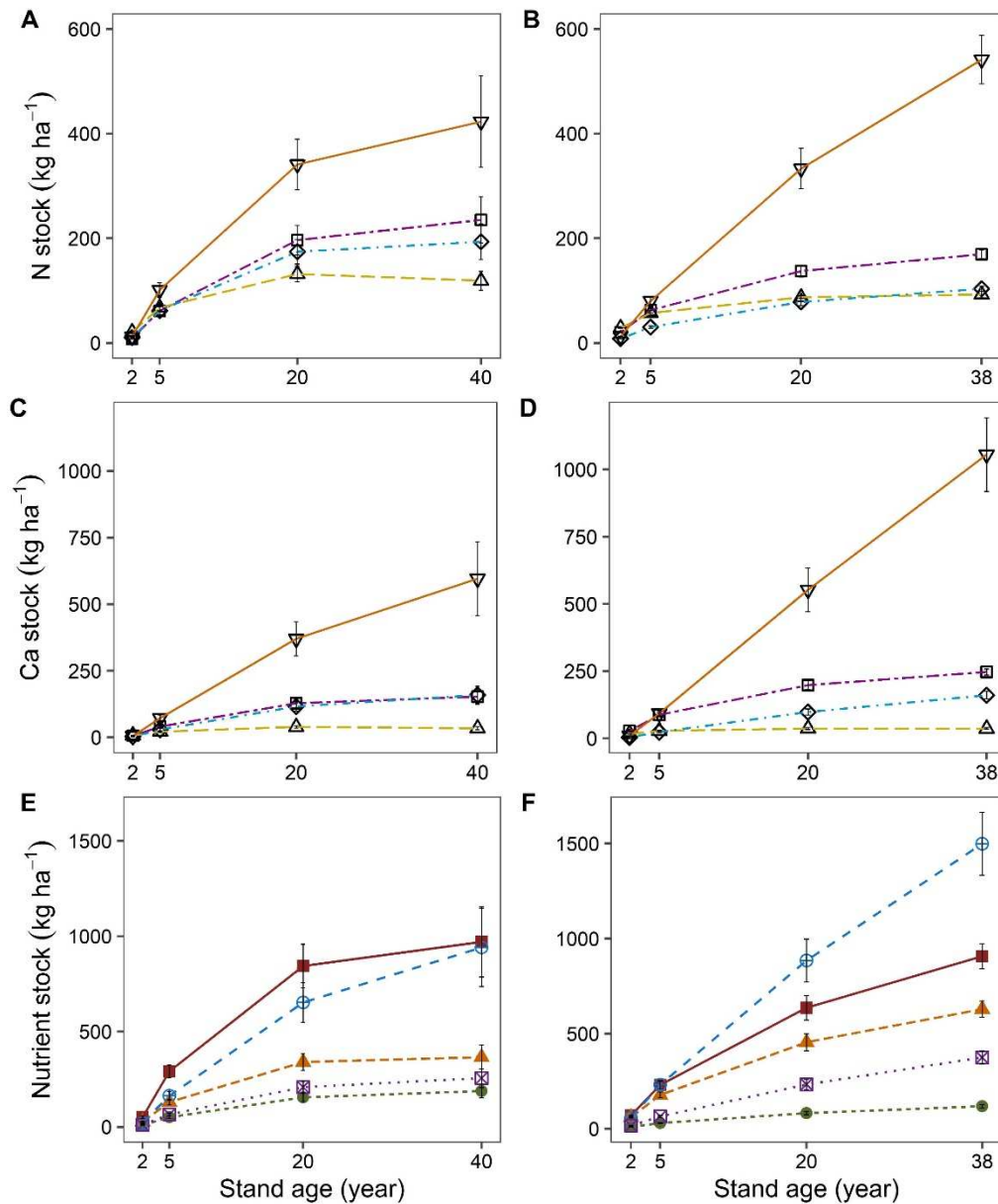


Figure 4: Dynamics of nutrient accumulation (in kg ha<sup>-1</sup>) for nitrogen at SAPH (A) and SOGB (B), calcium at SAPH (C) and SOGB (D) within tree components and in the whole tree at SAPH (E) and SOGB (F), throughout the chronosequence (n=4). Results were obtained from the allometric equations.

Caption Figure 5.A, B, C, D

- Branch
- △ Leaf
- ◇ Stump
- ▽ Trunk

Caption Figure 5.E, F

- N
- P
- ▲ K
- ⊕ Ca
- ⊗ Mg

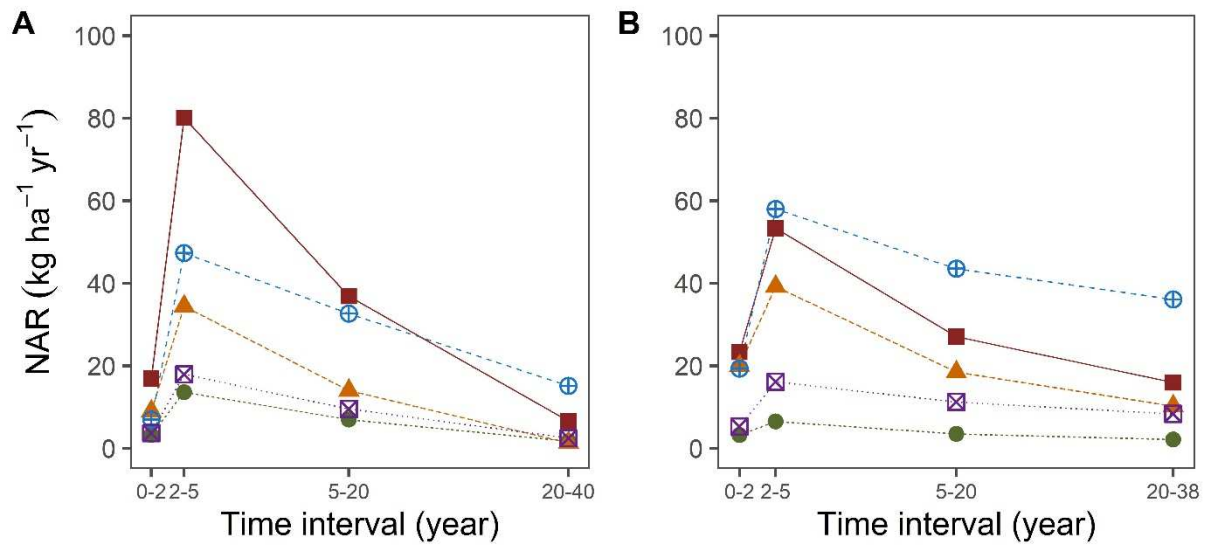


Figure 5: Nutrient accumulation rates (NAR, expressed in  $\text{kg ha}^{-1} \text{yr}^{-1}$ ) within stands throughout the chronosequence at SAPH (A) and SOGB (B).

Caption:



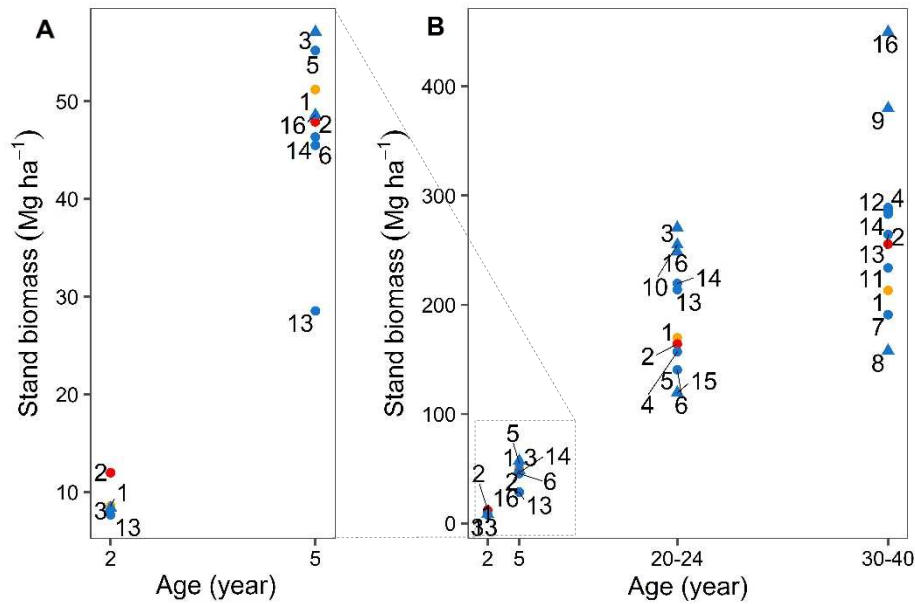


Figure 6: Dynamics of biomass accumulation in rubber stands according to 14 references plus our 2 study sites focusing on early growth (A) or on the whole cycle (B). Circles refer to studies using allometric equations to estimate stand biomass. Triangles refer to studies that estimated stand biomass by multiplying the biomass of the sampled trees by the stocking density. (1) SAPH; (2) SOGB; (3) Shorrocks (1965); (4) Hytönen et al. (2018); (5) Khamyong et al. (2011); (6) Yang et al. (2017); (7) Munasinghe et al. (2014); (8) Yew (2001); (9) Polinière and Van Brandt (1964); (10) Sivanadyan et al. (1995); (11) Méndez et al. (2012); (12) Brahma et al. (2018); (13) Wauters et al. (2008); (14) Petsri et al. (2013); (15) Zhang et al. (2016); (16) Samarappuli (1996).

Caption:

- Allometric equation
- ▲ Other method
- SAPH
- SOGB
- Reference data

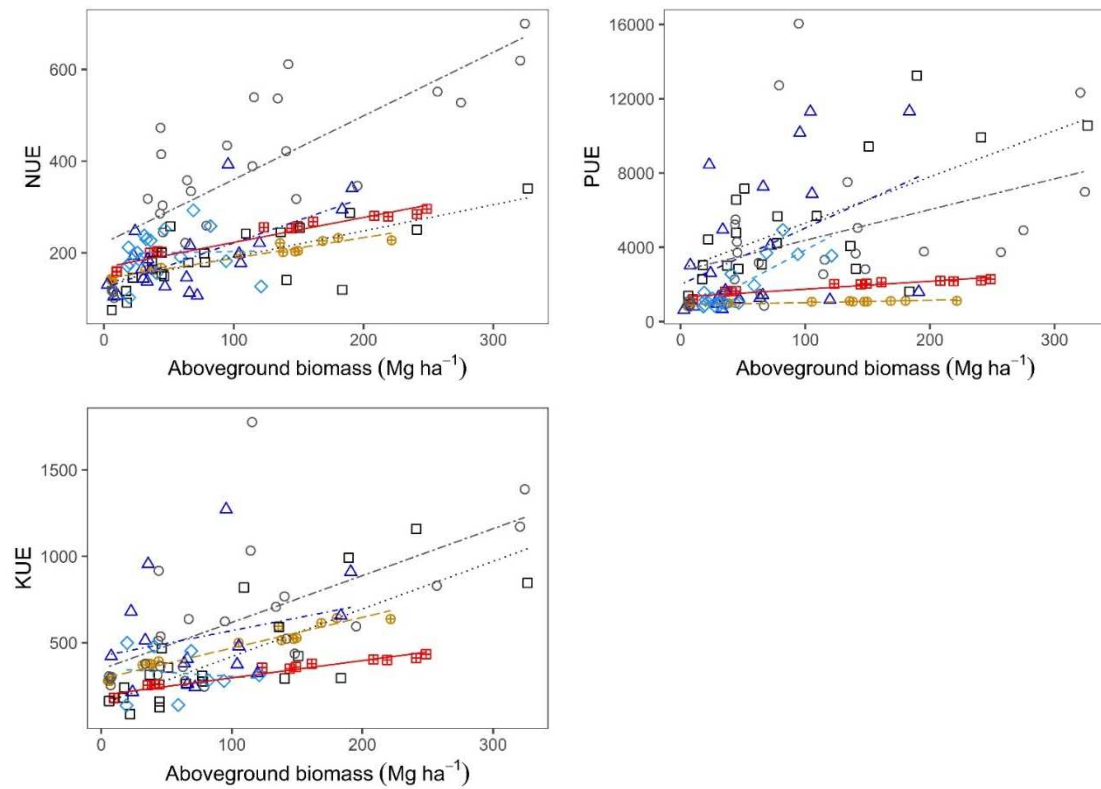


Figure 7: Relationships between aboveground biomass and nitrogen use efficiency (NUE), phosphorus use efficiency (PUE) and potassium use efficiency (KUE) at the SAPH and SOGB sites compared to four reference trees from Inagaki and Tange (2014): *Eucalyptus*, *Acacia*, other non-nitrogen fixing broadleaved trees (ONNFB) and N<sub>2</sub> fixing trees excluding *Acacia*.

Caption:

- Acacia trees
- Eucalyptus trees
- △ N<sub>2</sub> fixing trees ex. Acacia
- ◇ ONNFB trees
- ⊕ SAPH
- ⊞ SOGB

Table 1: Main soil characteristics in the upper layers (0-30 cm) in the reference plots of the chronosequence at SAPH and SOGB.

Site	Plot age (yr)	pH (H <sub>2</sub> O) <sup>a</sup>	Total C <sup>b</sup> (%)	Total N <sup>b</sup>	P <sup>c</sup> (ppm)	K <sup>d</sup> (cmol kg <sup>-1</sup> )	Ca <sup>d</sup>	Mg <sup>d</sup>	Clay (%)	Silt	Sand
SAPH	2	4.7	0.79	0.05	1.9	0.03	0.43	0.17	9.0	5.0	83.7
	5	5.8	0.99	0.05	3.6	0.02	1.57	0.26	6.5	13.8	79.0
	20	4.8	1.35	0.10	1.3	0.03	0.22	0.17	10.4	12.0	79.2
	40	4.3	0.76	0.06	8.7	0.02	0.25	0.06	10.3	2.1	87.4
SOGB	2	4.9	0.97	0.06	2.9	0.05	0.65	0.35	23.8	27.9	47.5
	5	5.7	0.84	0.07	2.7	0.07	3.89	0.63	25.4	12.4	60.1
	20	4.9	1.33	0.10	2.5	0.04	0.56	0.22	19.1	11.4	66.9
	38	4.7	1.08	0.09	5.4	0.04	0.30	0.12	19.0	15.3	65.9

<sup>a</sup> ratio 1:5

<sup>b</sup> by elemental analyser (FlashSmart™, ThermoFisher)

<sup>c</sup> ion exchange resin method, after extraction and dosage to vanado-molybdate

<sup>d</sup> ammonium acetate method (pH 7)

Table 2: Main characteristics of the stands studied in the two chronosequences, at SAPH and SOGB. Standard deviation among the 3 additional plots are indicated for survival rates, circumferences and tree density at planting.

Site	Plot type	Age (yr)	Survival rate (%)	Mean circumference (cm)	Density at planting (tree ha <sup>-1</sup> )	Tree spacing (m) and planting design	N-P-K-Ca-Mg added since planting (kg ha <sup>-1</sup> )
SAPH	Reference	2	94	18.1	555	6x3 (SR <sup>a</sup> )	70-22-72-82-155
	Additional	2	99 ± 1	17.3 ± 1.2	555 ± 0	6x3 (SR)	70-22-72-82-155
	Reference	5	83	43.1	555	6x3 (SR)	101-31-106-113-214
	Additional	5	90 ± 4	46.0 ± 2.2	555 ± 0	6x3 (SR)	101-31-106-113-214
	Reference	20	87	72.3	476	6x3.5 (SR)	101-31-106-113-214
	Additional	20	87 ± 4	78.3 ± 1.7	555 ± 0	6x3 (SR)	101-31-106-113-214
	Reference	40	66	101.6	500	8x2.5 (SR)	101-31-106-113-214
	Additional	40	54 ± 1	98.0 ± 2.9	511 ± 19	5-8x2.5-4 (SR)	101-31-106-113-214
SOGB	Reference	2	98	19.0	500	8x2.5 (SR)	90-18-76-40-61
	Additional	2	95 ± 0	19.4 ± 0.4	500 ± 0	13-3x2.5 (DR <sup>b</sup> )	90-18-76-40-61
	Reference	5	98	44.7	500	13-3x2.5 (DR)	300-61-250-133-205
	Additional	5	89 ± 3	43.8 ± 1.8	500 ± 0	13-3x2.5 (DR)	300-61-250-133-205
	Reference	20	79	85.0	500	13-3x2.5 (DR)	570-151-520-133-205
	Additional	20	74 ± 12	86.0 ± 8.3	500 ± 0	13-3x2.5 (DR)	570-151-520-133-205
	Reference	38	63	103.7	500	8x2.5 (SR)	917-267-867-133-205
	Additional	38	56 ± 6	111.9 ± 7.3	555 ± 0	6x3 (SR)	917-267-867-133-205

<sup>a</sup> single-row planting

<sup>b</sup> double-row planting

Table 3: Nutrient concentrations in tree components depending on the site and stand age (standard deviations are given in brackets). Different letters indicate significant differences between stand ages at the same site (Tukey post-hoc test with  $p < 0.05$ ).

Site	Stand age (yr)	Tree component	Nutrient concentration (%)				
			N	P	K	Ca	Mg
SAPH	2	Trunk	0.54 (0.06) a	0.09 (0.01)	0.27 (0.07) a	0.08 (0.01) b	0.10 (0.02) ab
	5		0.40 (0.06) b	0.07 (0.02)	0.17 (0.03) b	0.09 (0.02) b	0.10 (0.02) ab
	20		0.19 (0.03) c	0.06 (0.01)	0.07 (0.01) c	0.11 (0.01) b	0.07 (0.01) b
	40		0.38 (0.06) b	0.08 (0.03)	0.18 (0.03) b	0.59 (0.21) a	0.13 (0.04) a
SOGB	2	Trunk	0.32 (0.03) a	0.04 (0.00) b	0.30 (0.02) a	0.12 (0.04) b	0.12 (0.01) b
	5		0.35 (0.04) a	0.04 (0.01) b	0.24 (0.03) b	0.11 (0.02) b	0.10 (0.02) b
	20		0.22 (0.03) b	0.03 (0.00) c	0.17 (0.02) c	0.24 (0.05) b	0.10 (0.02) b
	38		0.34 (0.06) a	0.05 (0.01) a	0.24 (0.03) b	0.90 (0.33) a	0.16 (0.03) a
SAPH	2	Branch	1.13 (0.13) a	0.21 (0.01) a	0.79 (0.28) a	0.66 (0.20) a	0.19 (0.03) a
	5		0.70 (0.12) b	0.13 (0.03) b	0.27 (0.11) b	0.41 (0.16) b	0.14 (0.04) b
	20		0.31 (0.07) c	0.08 (0.02) c	0.10 (0.03) b	0.19 (0.03) c	0.07 (0.01) c
	40		1.07 (0.18) a	0.18 (0.03) a	0.30 (0.07) b	0.59 (0.13) ab	0.12 (0.03) b
SOGB	2	Branch	0.54 (0.03) a	0.08 (0.01) a	0.69 (0.15) a	0.71 (0.20) ab	0.14 (0.02) a
	5		0.58 (0.04) a	0.07 (0.01) ab	0.61 (0.11) a	0.54 (0.12) ab	0.11 (0.00) b
	20		0.29 (0.03) b	0.04 (0.01) b	0.27 (0.09) b	0.35 (0.10) b	0.07 (0.02) c
	38		0.55 (0.15) a	0.07 (0.03) a	0.27 (0.12) b	0.86 (0.33) a	0.13 (0.02) ab
SAPH	2	Leaf	3.2 (0.21) a	0.28 (0.04)	1.06 (0.15) a	1.12 (0.08) a	0.33 (0.05) b
	5		2.94 (0.21) ab	0.26 (0.04)	0.85 (0.18) ab	1.13 (0.21) a	0.42 (0.02) a
	20		2.34 (0.19) b	0.28 (0.08)	0.51 (0.07) c	0.74 (0.09) b	0.36 (0.08) ab
	40		3.00 (0.56) a	0.25 (0.06)	0.76 (0.16) b	0.72 (0.15) b	0.25 (0.05) c
SOGB	2	Leaf	2.28 (0.19) b	0.17 (0.02) ab	1.13 (0.15) b	1.53 (0.37) a	0.27 (0.02)
	5		2.65 (0.23) a	0.19 (0.01) ab	1.00 (0.20) b	1.36 (0.16) a	0.32 (0.03)
	20		2.68 (0.18) a	0.20 (0.01) a	1.45 (0.10) a	0.90 (0.14) b	0.30 (0.06)
	38		2.48 (0.20) ab	0.16 (0.04) b	0.70 (0.20) c	0.97 (0.15) b	0.31 (0.05)
SAPH	2	Root	0.53 (0.02)	0.12 (0.01)	0.25 (0.02) ab	0.14 (0.03)	0.11 (0.01)
	5		0.49 (0.17)	0.10 (0.03)	0.38 (0.13) a	0.23 (0.08)	0.10 (0.04)
	20		0.31 (0.01)	0.09 (0.01)	0.10 (0.02) b	0.14 (0.05)	0.12 (0.03)
	40		0.63 (0.22)	0.09 (0.03)	0.28 (0.10) ab	0.63 (0.46)	0.18 (0.09)
SOGB	2	Root	0.44 (0.02)	0.06 (0.01)	0.35 (0.02)	0.22 (0.08) b	0.09 (0.02)
	5		0.52 (0.04)	0.07 (0.02)	0.32 (0.12)	0.16 (0.02) b	0.11 (0.01)
	20		0.35 (0.02)	0.05 (0.01)	0.20 (0.01)	0.29 (0.06) b	0.16 (0.01)
	38		0.40 (0.09)	0.06 (0.02)	0.31 (0.15)	0.85 (0.38) a	0.31 (0.13)

Table 4: Nutrient removal in different harvesting scenarios (in kg ha<sup>-1</sup>) estimated from the allometric equations. The percentage of total nutrient accumulation in the trees removed by harvesting is given in brackets. Different letters indicate significant differences between scenarios at the same site (Tukey post-hoc test with  $p < 0.05$ ).

Site	Scenario	Nutrient removal (kg ha <sup>-1</sup> )				
		N	P	K	Ca	Mg
SAPH	1. Trunk only exported	423 c (42%)	103 b (52%)	186 c (48%)	596 (60%)	149 b (58%)
	2. Trunk and branches exported	658 bc (68%)	147 ab (73%)	254 bc (69%)	749 (78%)	184 ab (72%)
	3. Trunk, branches and stump exported	851 ab (88%)	177 a (94%)	337 ab (92%)	908 (96%)	243 a (95%)
	4. Whole tree exported (including stump)	970 a (100%)	188 a (100%)	366 a (100%)	942 (100%)	256 a (100%)
SOGB	1. Trunk only exported	541 c (61%)	75 c (64%)	418 c (66%)	1055 b (72%)	257 b (69%)
	2. Trunk and branches exported	732 b (79%)	97 b (82%)	524 b (83%)	1302 ab (88%)	297 b (80%)
	3. Trunk, branches and stump exported	815 ab (90%)	112 a (95%)	597 a (95%)	1462 a (98%)	363 a (97%)
	4. Whole tree exported (including stump)	908 a (100%)	118 a (100%)	628 a (100%)	1498 a (100%)	375 a (100%)